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SKELETON AND MUSCULATURE OF THE THORAX OF
GELASTOCORIS OCULATUS (FABRICIUS)
(HEMIPTERA-HETEROPTERA)

By MARGARET C. PARSONS
Harvard Biological Laboratories

CAMBRIDGE, MASS., U.S.A.

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No. 7 — *Skeleton and Musculature of the Thorax of
Gelastocoris oculatus (Fabricius)
(Hemiptera-Heteroptera)*

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INTRODUCTION

The members of the family Gelastocoridae are predaceous, littoral insects which live in swamps or along the shores of ponds and streams. The family is comprised of only two genera, *Gelastocoris* and *Nertha*. They are commonly called "toad bugs" because of their jerky, hopping means of locomotion, their roughened exoskeleton, and their prominent, laterally projecting compound eyes.

In a previous paper (Parsons, 1959) the author has described the cephalic skeleton and musculature of *Gelastocoris oculatus*. The study of the anatomy of this insect was undertaken for two reasons. First, except for those characters which are of taxonomic interest, almost nothing was known of the morphology of the Gelastocoridae. The few earlier works on the biology and taxonomy of this family are briefly reviewed in my previous paper.

Secondly, the Gelastocoridae, along with the closely related shore-dwelling families Ochteridae and Saldidae, occupy a basic position in previous theories of the evolution of the aquatic and semi-aquatic Heteroptera. These families are generally believed to represent an intermediate stage in the evolution of the water bugs from terrestrial forms. The various phylogenetic schemes which have been proposed have been based upon relatively few anatomical features, most, if not all, of which are external. It appeared, therefore, that a thorough study of both the external and internal morphology of one of the littoral Heteroptera might reveal additional evidence which could clarify the phylogenetic position of this group. *Gelastocoris* was used for this study because it could be obtained in large numbers and because it proved to be an excellent, easily kept laboratory animal.

The present study was greatly facilitated by the previous work of Larsén. That author has published many excellent papers on the thorax of the Heteroptera, and the two works (1945a and b) in which he described and compared in detail the thoracic skeleton and musculature of representatives of a great many different families are especially helpful. Previous to Larsén's studies there were very few works on the heteropteran thorax. Tower (1913) described briefly the external appearance of the thorax in *Anasa*, and Taylor (1918) discussed the thoracic sclerites of several families of Heteroptera, but included little detail. Hamilton (1931) studied the skeleton and musculature of the thorax of *Nepa* rather superficially. A much more extensive description of the skeleton and musculature was given by Malouf (1933) in his well illustrated paper on the thorax of *Nezara*. Rawat (1939) also briefly described both the muscles and the sclerites of this region in *Naucoris*. More recently Griffith (1945) and Esaki and Miyamoto (1955) have described the thoracic skeletons of *Ramphocoris* and the Veliidae respectively. Three other studies have been made which include both the skeleton and the musculature: these are the works of Sprague (1956) on *Hydrometra*, Akbar (1957) on *Leptocoris*, and Lauck (1959) on *Lethocerus*. The latter study is particularly valuable for its brief but thorough description of the musculature.

The author is indebted to Mr. Edwin P. Marks, of Washburn University, and to the members of the C. V. Riley Entomological

Society, of Columbia, Missouri, who provided the insects used in the present study. I also wish to thank Professor Frank M. Carpenter and my husband, Dr. Thomas S. Parsons, both of Harvard University, for their helpful advice and for their critical examination of the manuscript. This study was carried out during the tenure of the Ellen C. Sabin Fellowship, awarded by the American Association of University Women.

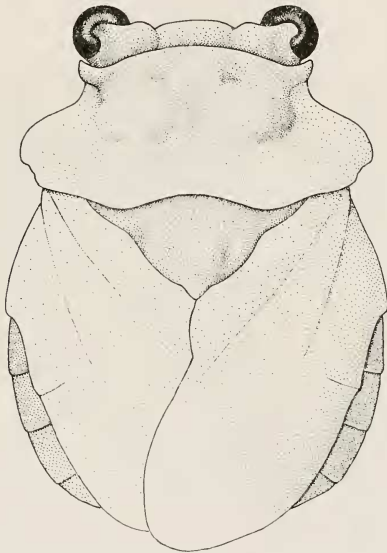


Figure 1. Dorsal view of *Gelastocoris oculatus*, legs removed. About 11X.

MATERIALS AND METHODS

Since *Gelastocoris* is a fairly large insect (approximately 6 to 8 mm. long), the skeleton and musculature could be studied by means of dissection under a stereoscopic microscope. Most of the dissections were made upon insects preserved in alcoholic

Bouin's solution, 10 per cent formalin, or Kahle's solution, and stored in 70 per cent alcohol. Since fresh material was sometimes needed, live gelastocorids were kept in the laboratory. The conditions under which they were kept have been described in a previous paper (Parsons, 1959).

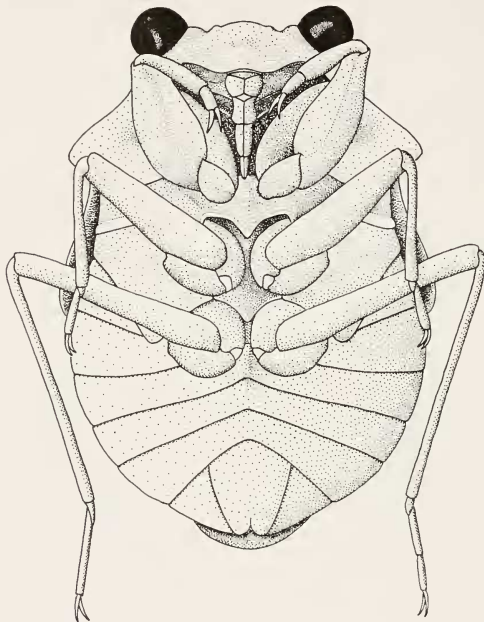


Figure 2. Ventral view of *G. oculatus* female, spines and hairs of legs omitted.

SKELETON

PROTHORAX

Cervical region. The cervical region of *Gelastocoris* is relatively simple. A *cervical membrane (CM)*, devoid of cervical sclerites, connects the postocciput of the head with the inturned anterior

margin of the prothorax (Fig. 5). The latter forms a tight collar around the postocciput. Two short tendons extend from the mid-dorsal region of the cervical membrane into the thorax. From the posterior margin of the postocciput, two pairs of apodemes project into the thorax, providing points of attachment for muscles. The longer of these, the *occipital condyles* (*O*), extends dorsally from the ventrolateral regions of the postocciput. Dorsal to them are the much shorter *lateral apodemes* (*L*), which project posteroventrally.

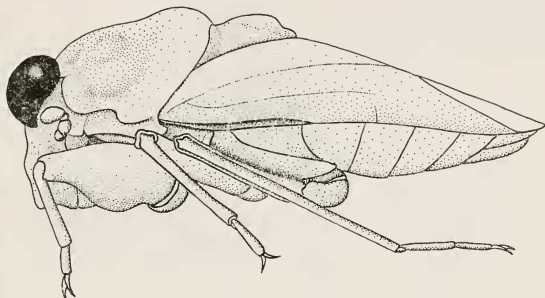


Figure 3. Lateral view of *G. oculatus* female.

Tergum. The prothoracic tergum is a large plate covering much of the anterior half of the body dorsally (Fig. 1). Much of its area is due to marginal evaginations, and the actual prothoracic cavity is comparatively small. These evaginations produce lobes which overlap the postocciput anteriorly and the mesonotum posteriorly. They are especially pronounced along the posterior and posterolateral tergal margins, where they form a broad *posterior protergal lobe* (*LP*) (the "tergal flap" of Malouf, 1933, and the "Hinterlappen" of Larsén, 1945a and b) shielding the anterior part of the mesonotum. The anterolateral lobes of the protergum are concave anteriorly, conforming to the shape of the head at the bases of the compound eyes. The two walls of all these marginal evaginations are fused together and appear as a single layer. A pronounced *transverse ridge*

(*TR*) ("Querleiste" of Larsén, 1945a and b) marks the anterior border of the posterior lobe and the posterior limit of the prothoracic cavity (Figs. 5 and 6). This ridge is a continuation of the ventral layer of the posterior lobe; attached to it is the intersegmental membrane (*I*) joining the prothorax to the mesothorax.

Pleuron. The boundary between the pleuron and the marginal tergal evaginations is not clear externally. A short *pleural suture* (Fig. 4, *PS*) separates the small *episternum* (*ES*) from the larger *epimeron* (*EP*). The ventral regions of each of these are evaginated to form *supracoxal lobes* (*EPS* and *ESS*) ("epimeral and

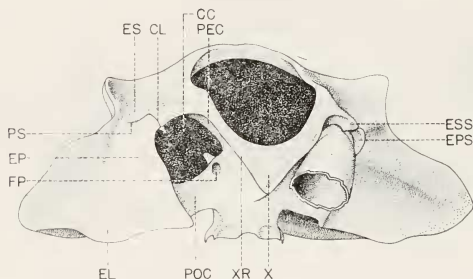


Figure 4. Ventral view of the prothorax, tilted slightly to the left. The muscles and the right leg have been removed; the left leg is cut off near the distal end of the coxa.

episternal flaps" of Malouf, 1933, and Akbar, 1957; "Supracoxallappen" of Larsén, 1945a and b) overlapping the bases of the *coxae*. The episternal and epimeral supracoxal lobes are separated by a pronounced *coxal cleft* (*CL*), which extends dorsally to the *coxal process* (to be described below). Externally the coxal cleft appears to be a ventral extension of the pleural suture; internally the cleft and the suture are separated by the coxal process. The posterior margin of the epimeron forms a large *posterior epimeral lobe* (*EL*) (the "lateral epimeral flap" of Malouf, 1933), which covers much of the mesothoracic epimeron as well as the bases of the forewings (Figs. 4, 5, and 6). Laterally, this lobe is continuous with the posterior lobe of the protergum,

the point of junction being braced by a U-shaped sclerotized strut (Fig. 5, *ST*). The anterior margin of the inner wall of the epimeral lobe is turned dorsally to form the ventral part of the transverse ridge, which medially becomes quite low and continues into the *posterior sternal process* (to be described below) (Fig. 6).

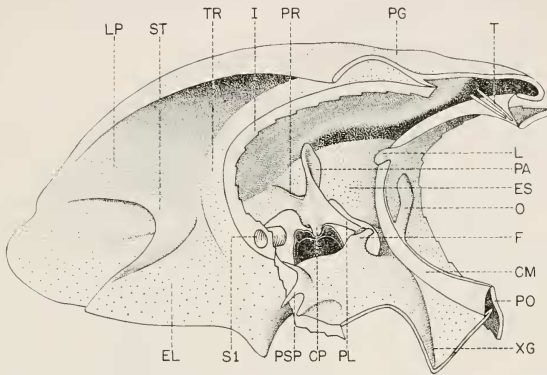


Figure 5. Posteromedial view of the left half of the prothorax and of the postocciptal region of the head. The tendons of the pericoxal membrane and the muscles have been removed.

The large *coxal cavity* (*CC*) is bordered laterally by the epimeron and episternum and medially by the sternum (Fig. 4). Anterior to the coxal cavity the episternum meets the sternum, forming a narrow *precoxal bridge* (*PEC*); posteriorly the fused epimeron and a sternum form a broad *postcoxal bridge* (*POC*). There is no clear boundary between the sternal and pleural elements. A view of the inner surface of the pleuron (Figs. 5 and 6) shows that the short pleural suture produces a distinct *pleural ridge* (*PR*) internally. At the end of the ridge is a strong *coxal process* (*CP*) ("coxal articulation" of Griffith, 1945; "Hüftgelenkkopf" of Larsén, 1945 a and b; "pleural articular process" of Akbar, 1957) which projects a short distance into the coxal cavity

and articulates with the base of the coxa. Just dorsal to the coxal process is a large, lamellar *pleural apophysis* (*PA*) ("pleural arm" of many authors; "Pleuralhaken" of Larsén, 1945a and b) which extends dorsally nearly to the lateral part of the notum. It does not fuse with the latter, as it does in many water bugs. A thick membrane (*Fig. 5, PL*) projects medially from the pleural apophysis to the *furca* (to be described below). A similar connection between the prothoracic pleural apophysis

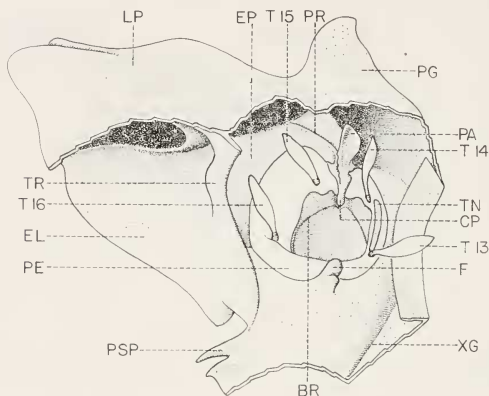


Figure 6. Dorsomedial view of the left half of the prothorax. The muscles and the pleurosternal bridge have been removed, and much of the medial part of the protergum has been cut away.

and the furca has been described in *Corixa* and *Salda* by Larsén (1945a and b), and in *Ramphocorixa* by Griffith (1945); the latter author termed it the *pleurosternal bridge*, and that term will be used here.

Sternum. The anterior part of the sternum is produced into a large triangular process which lies between the coxae (*Fig. 4, X*). A similar process in the metathorax of Heteroptera has been termed the *xiphus* by many authors, and that term will be used for this prothoracic structure. Along the posteroventral edge of

the xiphus runs a sharp, V-shaped ridge (Fig. 4, *XR*) which produces a groove internally (Figs. 5 and 6, *XG*). Laterally this ridge, which will here be called the *xiphal ridge*, continues into the precoxal bridge and runs along the posterior edge of the supracoxal lobe of the episternum, ending at the coxal cleft. The xiphal ridge corresponds to the "external ridge of the basisternum" of Akbar (1957); since it does not pass through the bases of the furcae, it probably does not represent a sternacostal suture. Akbar (1957) found a sternacostal suture posterior to this ridge in the prothorax of *Nezara*; in *Gelastocoris* there is no visible prothoracic sternacostal suture.

Just medial to the coxal cavities, on either side of the midline, are the short, thick sternal apophyses or *furcae* ("anterior endosternites" of Rawat, 1939; "Furcaäste" of Larsén, 1945a and b) (Figs. 5 and 6, *F*). Externally their positions are marked by the *furcal pits* (Fig. 4, *FP*). As Larsén (1945b) has pointed out, the term "furcal branch" is preferable to that of "furca" in the Heteroptera, since the furca is a single medial structure in many higher insects; the paired apophyses of the Heteroptera probably represent the branches of the single furca of other insects. For convenience, however, the term "furca" will be used here. The prothoracic furcae of *Gelastocoris* are each subdivided into a lateral and a medial arm.

The posterior part of the sternum projects into the cavity of the mesothorax as a broad plate. Lateral to this plate are two prong-like *posterior sternal processes* (*PSP*), which are continuous with the ventral part of the transverse ridge (Figs. 5 and 6). In some specimens these processes are heavily sclerotized, while in others they appear to be more or less membranous. They may represent the "posterior horn-like processes" or "spina" of Akbar (1957), and the "posterior prothoracic endosternites" of Rawat (1939). Lauck (1959), like Rawat, believed them to be part of the furcae. Both Akbar (1957) and Larsén (1945b), however, considered them to represent the spina of other insects; the latter author observed these processes in several aquatic and terrestrial Heteroptera. Just lateral to the posterior sternal processes, in the intersegmental membrane between the prothorax and mesothorax, lies the large *first thoracic spiracle* (Fig. 5. *S1*).

PTEROTHORAX

The mesothorax and metathorax, unlike the prothorax and mesothorax, are bound closely together, the intersegmental membrane being either very narrow or, more commonly, entirely absent. In the following discussion the two segments will be considered together.

TERGUM

Mesothorax. On the anteromedial portion of the mesothoracic tergum is the semicircular *first phragma* (Figs. 7 and 10, *P1*) (“prephragma” of Akbar, 1957), an invagination which extends

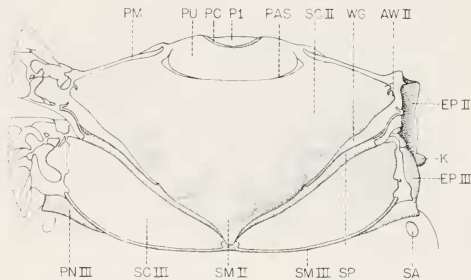
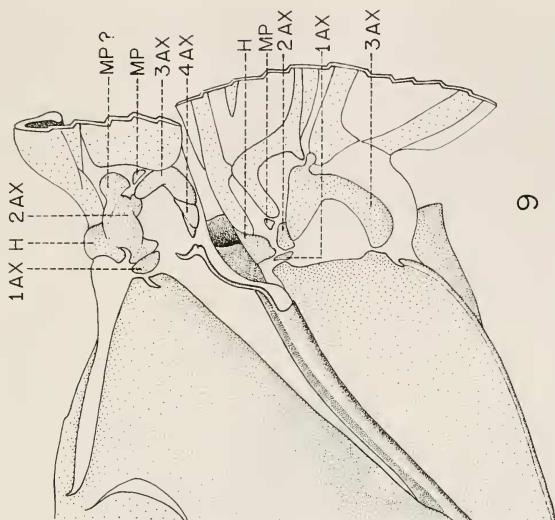


Figure 7. Dorsal view of the pterothorax. The wings have been removed from the right side, and the wings of the left side have been extended and cut off near their bases.

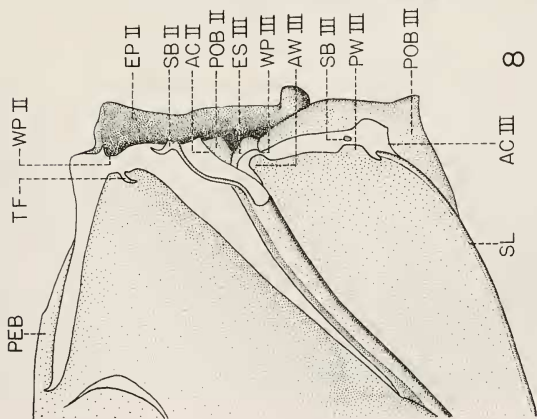
anteroventrally into the thoracic cavity. The two thin layers of the invagination are closely apposed, the intersegmental membrane from the prothorax attaching along the posterior edge of the more dorsal layer (Fig. 10). A narrow sclerotized *precosta* (*PC*) is present where the membrane meets the margin of the phragma, and medially two slender tendons extend anteriorly from the ventral surface of the membrane (Fig. 7).

Posterior and lateral to the first phragma lies the *mesonotum*. A broadly U-shaped *parapsidal suture* (Figs. 7 and 10, *PAS*) (“parapside” of Malouf, 1933; “pre-scutal suture” of Rawat, 1939; “convergent suture” of Lauck, 1959) separates an antero-medial *precutum* (*PU*) (“scutum” of Malouf, 1933, and Lauck,



9

Figure 9. Dorsal view of the right side of the pterothorax. The wings have been extended and cut off near their bases.



8

Figure 8. Dorsal view of the right side of the pterothorax. The wings have been removed.

1959) from the rest of the mesonotum. The anterolateral margins of the prescutum are connected anteriorly to the mesothoracic episternum by the *prealar bridges* (Fig. 10, *PEB*), which are roughly V-shaped. The parapsidal suture ends just posterior to the prealar bridges; internally it produces a very low *parapsidal ridge* (Fig. 12, *PAR*). Medial to the parapsidal suture is a narrow membranous area which is most conspicuous laterally.

The rest of the mesonotum is made up of the *scutum* (*SC*) and *scutellum* (*SM*). No scutoscutellar suture is present to separate these regions; their boundaries can be determined only by the

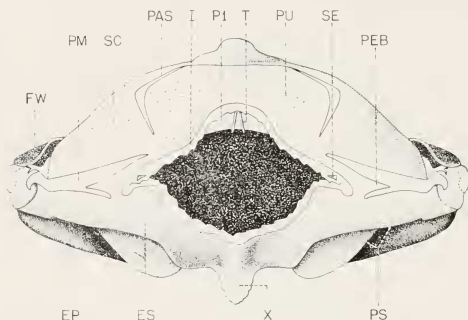


Figure 10. View of the anterior surface of the mesothorax.

insertions of the tergal muscles, which, according to Snodgrass (1927) arise only from the prescutellar area. According to this criterion, the scutellum is very narrow laterally but becomes wider medially. The scutum is bordered anteriorly by the parapsidal suture and by the *prealar membrane* (*PM*), which extends from the lateral edge of the prealar bridge into the membrane of the forewing (Figs. 7 and 10). Laterally, the scutum extends to the bases of the forewings on either side. Where it articulates with the base of the wing it is cleft by a posteriorly curved *tergal fissure* (Fig. 8, *TF*) ("Tergalspalt" of Larsén, 1945a and b). This fissure separates two small processes which together form the *anterior notal wing process* (Fig. 7, *AWII*) ("anterior wing

process" of Rawat, 1939). The more anterior process has been termed the "vectis dorsualis anterior" (Malouf, 1933), the "vorderen Tergalhebel" (Larsén, 1945a) and the "anterior notal wing process" (Akbar, 1957), while the more posterior process has been called the "vectis dorsualis posterior" (Malouf, 1933) and the "hinteren Tergalhebel" (Larsén, 1945a).

The scutellum ("scutoscutellum" of Lauek, 1959) is the posterior region of the mesonotum, which medially covers much of the metatergum. Since the latter is concealed by the forewings and since the anterior part of the mesoscutum is overlapped by the posterior lobe of the pronotum, only the mesoscutellum and the posterior part of the mesoscutum are normally visible dorsally (Fig. 1). The posterior apex of the scutellum has been termed the "scutellar flap" (Malouf, 1933) or the "Scutellarappen" (Larsén, 1945 a and b). Along the posterior part of the scutellum runs a deep *wing groove* (Fig. 7, *WG*) which receives the posterior margin of the forewing when the latter is at rest. Medially the wing groove is narrow and sclerotized, resembling a deep suture, but laterally it becomes wider and membranous, the membrane continuing into the forewing (this membranous part of the groove corresponds to the region labelled "X" in Fig. 3B of Rawat, 1939). The posterior wall of the wing groove, along with the narrow region of the scutellum posterior to it, forms the *scutellar process* (*SP*) ("processus scutellaris tertius alae" of Malouf, 1933; "narrow sclerotized strip" of Rawat, 1939; "Scutellumfortsatz" of Larsén, 1945 a and b; "lateral scutellar plate" of Akbar, 1957; probably the "frenum" of Tower, 1913). The surface of the scutellar process is somewhat lower than that of the scutellum proper. Laterally it narrows and bends anteriorly, becoming fused with the *subalare* (Fig. 8, *SBII*), an irregularly shaped sclerite lying in the posterior part of the base of the wing. Just behind the subalare is the *axillary cord* (*ACII*), which comes off from the scutellar process. Both Rawat (1939) and Akbar (1957) considered the lateral limit of the scutellar process to represent a posterior notal wing process. Larsén (1945b), however, claimed that the Heteroptera lack a posterior notal wing process, the wing instead articulating with the subalare; this is certainly the case in the mesothorax of *Gelastocoris*.

The *postnotum* ("pseudonotum" or "postscutellum" of many authors) is externally visible only laterally (Fig. 11, *PNII*). This lateral portion (the "Lateropostnota" of Larsén, 1945a and b) lies posteroventral to the subalare and axillary cord, and is continuous with the mesothoracic epimeron, forming the *postalar bridge* (Fig. 8, *POBII*) ("Postalare" of Taylor, 1918). The posterior margin of the postalar bridge is joined to the anterior edge of the metathoracic episternum, the boundary between the two being indistinct in many specimens. Medially the postnotum is concealed by the scutellar process, and the boundary between these two regions is also indistinct. A view of the inner surface

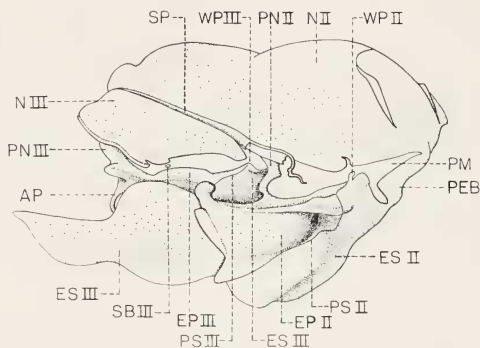


Figure 11. Lateral view of the right side of the pterothorax. The wings and legs have been removed.

of the tergum (Fig. 12) reveals that the medial part of the postnotum is extremely narrow. Posteriorly it becomes continuous with the anterior wall of the *second phragma* (*P2*) ("mesopostphragma" of Akbar, 1957), an invagination of the tergum between the mesothorax and metathorax. This is the largest of the three thoracic phragmata. Laterally it is a fairly low ridge which meets the pleuron at the boundary between the mesothoracic epimeron and the metathoracic episternum; medially it becomes much higher, and possesses, on either side of the midline, a *ventral*

process (V) ("ventrale Fortsatz of Larsén, 1945a and b). This process extends ventrally nearly to the mesosternal *furca* (FII) (to be described below); its two walls are not closely apposed and may be easily separated.

Metathorax. The metathoracic tergum is considerably shorter than the tergum of the preceding segment. This is true of most Heteroptera, since the main flight muscles are located in the mesothorax (Larsén, 1945b). The metathoracic tergum consists mainly of the *notum*, the *postnotum* being visible, as in the mesothorax, only dorsolaterally. Medially the notum is quite narrow and partially concealed by the mesoscutellum (Fig. 7), but laterally it becomes broader. Its anterior wall (the "prescutum" of Tower, 1913) is continuous medially with the posterior wall of the second phragma. Laterally the notum is separated from the phragma by a narrow membrane (concealed, in Figures 7-9, by the scutellar process). Larsén (1942) has pointed out that this separation enables the lateral edges of the metanotum to be bent downwards, indirectly causing the extension and raising of the hindwing. The lateral border of the metanotum bears both an *anterior* and a *posterior notal wing process* (Fig. 8, *AWIII* and *PWIII*), although Larsén (1945b) reported the latter to be absent in the Heteroptera. In the wing membrane ventral to the posterior notal wing process and the *third axillary sclerite* (to be described later) lies an extremely minute *subalare* which is easily overlooked (Figs. 8 and 11, *SBIII*).

The medial part of the metanotum bears a broadly U-shaped groove (Fig. 7) which produces a ridge on the inner surface. This groove appears to turn laterally just before the posterior notal border and to run to a point just behind the posterior notal wing process (Fig. 8). It may represent a *scutoscutellar suture* (*SL*) ("V-Leiste" of Larsén, 1945a and b). If so, the narrow notal region behind it may be termed the *scutellum* (*SMIII*) and the more extensive area anterior to it the *scutum* (*SCIII*). The posterolateral part of the scutellum resembles the scutellar process of the mesothorax. The *axillary cord* of the hindwing (Fig. 8, *ACIII*) comes off from the lateral edge of this region, but the subalare is not joined to the scutellum as it is in the mesothorax.

The medial part of the narrow postnotum (*PNIII*) is concealed by the notum; laterally it becomes somewhat broader and is visible dorsally (Fig. 7) and laterally (Fig. 11). It joins the meta-thoracic epimeron to form the *postalar bridge* (Fig. 8, *POBIII*) just posterior to the axillary cord. The posterior margin of the postnotum continues into the anterior wall of the *third phragma*; the latter, which marks the dorsal boundary between the thorax and abdomen, is a low ridge without ventral processes (Fig. 12, *P3*). It is much less pronounced than the second phragma.

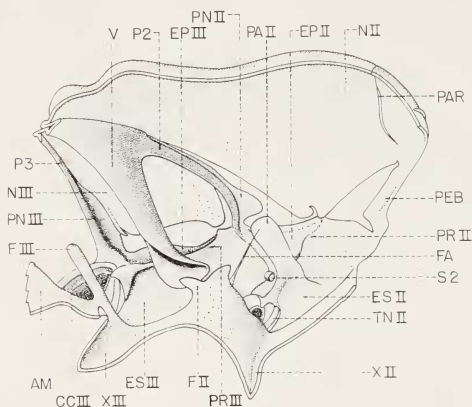


Figure 12. Medial view of the left half of the pterothorax, with the muscles removed. Only the bases of the coxae are shown.

PLEURON

Mesothorax. The intersegmental membrane (I) from the prothorax meets the pleuron of the mesothorax along the medial edge of the prealar bridge and the anterior margin of the mesothoracic *episternum* (Fig. 10). Within the membrane, just anterior to the most dorsal part of the prealar bridge, lies a very small sclerite (*SE*) which provides an insertion for one of the depressor muscles of the thorax. According to Larsén (1945b), this sclerite is a free lateral part of the first phragma.

A ventral view of the mesothorax (Fig. 13) shows an extensive episternum (*ESII*) and a somewhat smaller epimeron (*EP II*) separated by a long and distinct pleural suture (*PSII*). Both these sclerites have *supracoxal lobes* overlapping the coxal bases as in the prothorax; in addition, a *posterior lobe of the epimeron* (*ELII*), which is continuous with the epimeral supracoxal lobe, overlaps part of the metathoracic episternum, concealing the lateral boundary between the mesothoracic and metathoracic pleura (Fig. 14). At the posterolateral corner of this posterior epimeral lobe is a conspicuous knob (Figs. 7 and 14, *K*) ("Höcker" of Larsén, 1945a and b) which fits into a depression on the anterior margin of the forewing and thus holds the resting

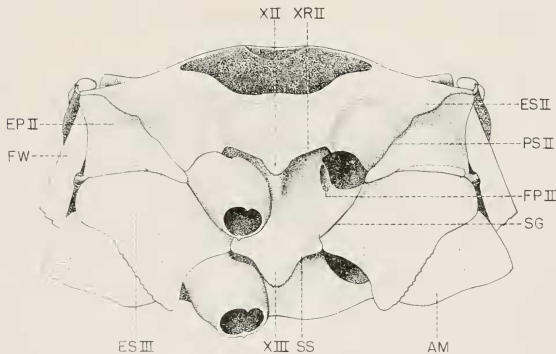


Figure 13. Ventral view of the pterothorax. The legs, except for the right coxae, have been removed and the forewings have been cut off near their bases.

wing firmly in place. Dorsal and considerably anterior to this knob, the epimeron meets the mesopostnotum forming the postalar bridge (Fig. 11).

Ventral to the base of the wing, both pleural sclerites are somewhat evaginated to form a sort of shelf; in the epimeron, this shelf continues into the posterior epimeral lobe (Fig. 11). Dorsal to this evaginated portion, at the point where the epimeron joins the episternum, is a short *pleural wing process* ("wing fulcrum" of Taylor, 1918) (Figs. 8 and 11, *WP II*). This process lies ventral and lateral to the anterior notal wing process. The dorsal margin of the epimeron is somewhat thickened and curved

medially, which helps to strengthen and support the pleural wing process.

The *coxal cavity* is bordered medially by the sternum and laterally by the pleural sclerites (Fig. 15). Anterior to it lies a very broad *precoxal bridge* where the episternum is fused indistinguishably with the sternum. It is difficult to determine whether or not a *postcoxal bridge* is present, since the boundary between the mesosternum and metasternum is uncertain. According to Larsén (1945b), the boundary between these two regions is marked by the mesosternal furcae. If this criterion is used, the mesosternal-metasternal boundary must lie just at or slightly behind the posterior margin of the mesocoxal cavity. If the former is true, the postcoxal bridge is absent; if the latter, the bridge is very narrow, probably being represented by the slight ridge bordering the posterior edge of the coxal cavity (Fig. 15, *RG*). On this ridge, one of the metathoracic muscles, *M. episterno-coxalis* (Muscle 66), originates. Larsén (1945a) considered the point of origin of this muscle to be the anterior part of the metathoracic episternum, immediately behind the intersegmental boundary. If such is the case, the mesothoracic postcoxal bridge must be absent.

At the lateral margin of the coxal cavity there is a conspicuous *coxal process* (Fig. 15, *CPII*) from which the distinct *pleural ridge* (*PRII*) runs anterodorsally on the inner surface of the pleuron (Figs. 12 and 15). There is no basicoxal plate ("freie Basicoxalplatte" of Larsén, 1945d). The entire length of the pleural ridge is visible. About midway along the pleural ridge is a rectangular *pleural apophysis* (*PAII*) (possibly the "basalare apodeme" of Akbar, 1957), which bends somewhat posterolaterally and extends towards the second phragma.

Metathorax. The metathoracic pleuron is composed mostly of the *episternum* (Fig. 13, *ESIII*) with its large *supracoxal* and *posterior lobes*. These lobes, which are continuous with each other, overlap part of the abdomen. The greatly reduced *epimeron* possesses no supracoxal lobe, and is visible only laterally (Fig. 11, *EPIII*). Anteriorly the episternum is covered by the posterior lobe of the mesothoracic epimeron. This lobe covers both the intersegmental boundary between the mesopleura and metapleura and the *second thoracic spiracle* (Figs. 12, 14, and 15, *S2*)

which is located at the anterior edge of the metathoracic episternum. The posterior margin of the mesothoracic epimeral lobe lies very closely upon the metathoracic episternum, and it seems unlikely that air could reach the spiracle from a posterior direction. Laterally, however, between the posterior lobe of the mesothoracic epimeron and the metathoracic episternum, there is a space which bears some resemblance to the "air chamber" of corixids, as described by Griffith (1945). The air reaching the second thoracic spiracle probably comes in through this space, which is located directly beneath the base of the hindwing. This condition is typical of the aquatic Heteroptera rather than the terrestrial bugs, as Larsén (1945b) has pointed out.

The *coxal cavity* is very large and oval in shape, its long axis running mediolaterally in relation to the body (Fig. 15). Anteriorly it is bordered by a very broad *precoxal bridge* which joins the episternum with the sternum, and anteromedially by the metasternum. Posteriorly and posteromedially it is bordered by the abdominal sternites. There is no postcoxal bridge or basicoxal plate. A very large *coxal process* (*CP III*) articulates laterally with the base of the *coxa*. This process has an anterior extension which articulates with the *trochantin* (*TN III*) (to be described later). Dorsal to the coxal process a high *pleural ridge* (*PR III*) extends anterolaterally for a short distance and then curves to run directly anteriorly, parallel to the longitudinal axis of the body (Fig. 15). Externally only the dorsal part of the *pleural suture* (*PS III*), which ends in the *pleural wing process* (*WP III*), is visible (Fig. 11); the ventral part of the suture is concealed by the lateral part of the metathoracic posterior episternal lobe. There is no pleural apophysis in the metathorax.

Across the precoxal bridge runs a deep *stink groove* (Fig. 14, *SG*) which produces a high *stink ridge* internally (Fig. 15, *SR*). The groove extends from the external orifice of the thoracic stink gland, at the base of the furca, to the point where the posterior mesothoracic epimeral lobe begins to overlap the metathoracic episternum. The part of the precoxal bridge, anterior to the groove corresponds to the "anterior laterale" plus the "basisternum" of Brindley (1934), the "basisternum" of Griffith (1945), and the "laterale" of Akbar (1957); the part posterior to the groove represents the "antecoxal laterale" of Brindley

(1934), the "episternum" of Griffith (1945), and the "antecoxal" of Akbar (1957). The anteromedial wall of the groove forms a narrow flap (Fig. 14, *AF*) (the "stink fold" of Akbar, 1957, and the "anterior laterale" of Brindley, 1934), which extends posteriorly, while the posterolateral wall forms an even larger flap (*PF*) in the lateral part of the groove. This second flap extends anteriorly and overlaps the smaller one. Together the two flaps form a partial covering over the ventral side of the groove, helping to hold the secretion in the channel. The form and position of the stink groove is more like that of the aquatic Heteroptera, as described by Larsén (1945b), than like that of

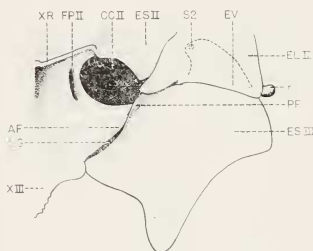


Figure 14. Ventral view of the posterior portion of the pterothorax, left side, showing the stink groove. The legs have been removed. The broken lines indicate the positions of the anterior metathoracic episternum and of the second thoracic spiracle, which are overlapped by the posterior lobe of the mesothoracic epimeron.

the terrestrial bugs; Larsén did not consider the stink grooves of these two groups to be homologous. There is an especially strong resemblance between the grooves of *Gelastocoris* and the Corixidae, the chief difference being that the corixids lack the larger of the two flaps.

Just beyond the lateral end of the stink groove, the posterior edge of the mesothoracic posterior epimeral lobe is modified to form a very smooth, shiny band (Fig. 14, *EV*), whose surface contrasts sharply with the rough texture of the rest of the sclerite. This band is so placed that the secretion emerging from the stink groove flows out upon it. It probably serves as an *evaporating*

surface for the secretion; to the author's knowledge, such an evaporating surface has not been reported in any other heteropteran.

The epimeron is largest in the anteroposterior direction. Posterodorsally it joins the postnotum to form the postalar bridge, and posterolaterally it is somewhat produced to form a posteriorly projecting lobe (the "epimeral flap" of Akbar, 1957) (Fig. 11). Just ventral to this lobe the epimeron is more or less fused with an anterolateral process from the abdomen (Figs. 11 and 15, *AP*). This process, the "Pleura des ersten Abdominalsegments" of Larsén (1945a) and the "epimeral fold" of Akbar (1957), bears the *first abdominal spiracle* at its base, and appears to be abdominal in nature; Snodgrass (1909) considered it to be part of the abdomen in *Benacus*.

STERNUM

Mesothorax. Like the prosternum, the mesosternum possesses an evaginated triangular *xiphus* between the coxae (Fig. 13, *XII*). Along the posteroventral edge of the xiphus runs a *xiphial ridge* (*XRII*) similar to that of the prothorax; internally it appears as a groove (Fig. 15, *XG*). Unlike the corresponding ridge of the prosternum, it does not reach the coxal cleft, but runs instead to the anteromedial border of the coxal cavity. Since it does not pass through the furcal bases, it probably does not represent a sternacostal suture.

Just medial to the coxal cavities lie the conspicuous, oval *furcal pits* (Figs. 13 and 14, *FP II*). They mark the broad bases of the large *furcae* (Figs. 12 and 15, *F II*). The latter possess anterior and posterior arms (together probably corresponding to the "posterior arm of the endosternite" of Rawat, 1939) which extend dorsally nearly to the ventral processes of the second phragma. From the more anterior furcal arm a long, slender *furcal apodeme* (*FA*) ("anterior arm of the endosternite" of Rawat, 1939; "Furcaapodem" of Larsén, 1945a and b; "anterior process of the furca" of Griffith, 1945; "lateral arm of the mesothoracic furca" of Lauck, 1959) extends dorsolaterally and nearly touches the tip of the pleural apophysis.

There is no clear boundary between the mesosternum and the metasternum. As has been previously mentioned, the mesosternal *furcae* probably indicate its approximate position.

Metathorax. The *xiphus* ("sternellum" of Griffith, 1945) of the metasternum is considerably larger than those of the preceding two segments (Fig. 13, *XVIII*). Along its posteroventral margin runs a ridge (*SS*) which resembles the xiphal ridges of the prothorax and mesothorax. Since it ends at the bases of the metathoracic furcae, however, it may represent a *sternocostal suture*. If so, the part of the sternum anterior to it may be termed the *basisternum*, and the short portion posterior and lateral to it (the posterodorsal wall of the xiphus) may be

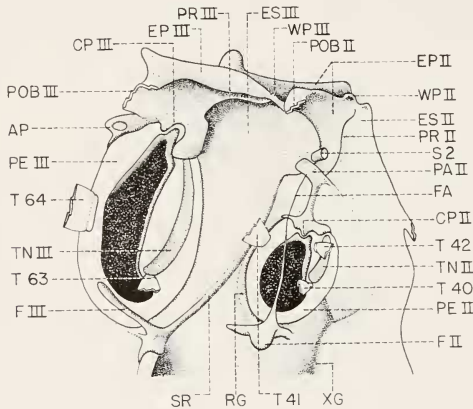


Figure 15. Dorsal view of the inner surface of the pterothorax, left side, showing the sterna and pleura. The pterotergum has been cut off at the postalar bridges and at the mesothoracic prealar bridge, and the tendons in the perioxal membranes have been cut off near their bases. The muscles have been removed.

called the *sternellum* or *furcasternum*. Extending between the metathoracic furcae is a membrane which separates the metathoracic sternum from the sternum of the first abdominal segment.

The *furcal pits* are concealed externally by the lateral edges of the xiphus. Internally the furcae appear as two unbranched processes (Figs. 12 and 15, *FIII*). They extend posterolaterally and are longer and much more slender than the mesothoracic furcae.

LEGS

The raptorial forelegs of *Gelastocoris* are oriented differently, with respect to the body, than are the walking and jumping pterothoracic legs. For convenience, however, the descriptive terms applied to the surfaces of the last two pairs of legs will be the same as those used for the corresponding surfaces of the forelegs. The terms "anterior" and "posterior" are here applied to the anteromedial and posterolateral sides of the foreleg respectively; "ventral" refers to the inner surfaces (those which

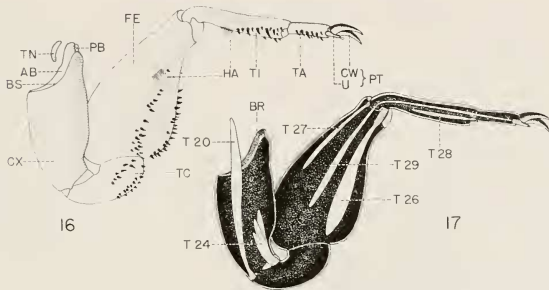


Figure 16. Medial view of the left prothoracic leg and trochantin.

Figure 17. Medial view of the inner surface of the left prothoracic leg, showing the tendons.

meet, on the femur and tibia, when the latter are apposed), and "dorsal" refers to the outer surfaces. The numbers used to designate the various tendons are the same as those of the muscles which insert on them.

Prothoracic legs (Figs. 6, 16, and 17). The prothoracic coxal cavity is fairly round. In the anterior part of the *pericoxal membrane* (*PE*) ("coxal corium" of Griffith, 1945, and Akbar, 1957) lies a small *trochantin* (*TN*), which does not appear to articulate with either the pleuron or the base of the *coxa*. The coxa is therefore articulated only at the coxal process, and this single joint allows it to move freely in all directions. Such freedom of movement is advantageous in a raptorial leg; Rawat

(1939) has reported a similar condition in the foreleg of *Naucois*. Four tendons in the pericoxal membrane provide insertions for the muscles which move the coxa; *Tendon 13* is located just medial to the medial end of the trochantin, to which it is partially attached, *Tendon 11* just lateral to the lateral end of the trochantin, *Tendon 15* slightly posterior to the coxal process, and *Tendon 16* in the posteromedial region of the pericoxal membrane.

The coxa (*CX*) is nearly cylindrical in form, and projects out farther from the body than do the coxae of the second and third pairs of legs. A *basicostal suture* (*BS*) encircles its proximal end; posteromedially the suture is very faint and close to the edge, but laterally it becomes clearer, producing a *basicostal ridge* (*BR*) ("basicosta" of Snodgrass, 1935) internally. It separates off an *anterior basicoxite* (*AB*) ("vorderes Basicoxale" of Larsén, 1945c) anterior to the coxal process, and an equally large *posterior basicoxite* (*PB*) ("hinteres Basicoxale" of Larsén, 1945c) posterior to that process. Snodgrass (1935) termed the posterior basicoxite the "meron"; Larsén (1945c and d), however, has shown that the posterior basicoxite and the meron are two separate elements, and that the latter is absent in the Heteroptera. Between the two basicoxites the basal coxal rim is invaginated to form a socket (the "articular process" of Griffith, 1945) into which the coxal process fits.

A dicondylic joint with anterior and posterior articulations joins the coxa with a short, curved *trochanter* (*TC*). On the ventral surface of the latter are two irregular rows of short spines. Two tendons, whose bases are attached to the proximal rim of the trochanter by tough membranes, extend into the coxa. The longer of these, *Tendon 20*, is located in the part of the rim which is farthest from the femur, and reaches into the thoracic cavity. A shorter, three-branched *Tendon 21* comes from the part of the rim nearest the femur.

A diceondylic joint with dorsal and ventral articulations joins the trochanter with the *femur* (*FE*). These two segments are joined so closely together that the condyles are difficult to see. The femur is greatly thickened to accommodate the powerful tibial muscles which originate on its inner walls. These muscles enable the *tibia* (*TI*) to open and close upon the femur. The femur is broadest proximally, the dorsal part of the segment

forming a hump above the articulation with the trochanter. The ventral surface of the femur is flattened, and an irregular row of stout spines extends along each side of the flattened area. On the anterior surface of the femur, just dorsal to the row of spines, is a comb of long, fine hairs (*HA*). This meets a similar comb of hairs on the tibia when the two segments are brought together. It probably serves, as Weber (1930) has suggested, as a cleaning organ for the head and antennae; the insects often perform "grooming" movements with their forelegs in the region of the head.

The femur and tibia are joined by a dicondylic joint with anterior and posterior articulations. The ventral surface of the tibia is flattened, and bears two rows of spines similar to those of the femur. When the tibia and femur are closed upon each other, prey may be caught between the apposed flattened areas and held in place by the spines. Two long tendons from the ventral (*Tendon 26*) and dorsal (*Tendon 27*) regions of the proximal edge of the tibia extend into the femur. The base of *Tendon 26* is expanded into a broad sclerotized plate (the "genuflexor plate" of Akbar, 1957) which is movably bound to the rim of the tibia.

The tibia and *tarsus (TA)* are joined primarily by a membrane, but have a weak anterior and posterior dicondylic joint. From the ventral region of the proximal edge of the tarsus, *Tendon 28* extends into the tibia. There is only one tarsal segment. Distally the tarsus is joined by a membrane to the *pretarsus (PT)*, which consists of two fairly long, stout *claws (CW)* and a ventral plate, the *unguitractor (U)* ("flexor plate" of Rawat, 1939). The distal end of the unguitractor is narrowed, and bears two very fine, short spines. Akbar (1957) reported similar spines in *Leptocoris* and suggested that they may be analogous with the "empodium" of Diptera. From the base of the unguitractor, a very long *Tendon 29* ("depressor apodeme" of Akbar, 1957) extends through the tarsus and tibia and into the femur.

Mesothoracic legs (Figs. 15 and 18). Unlike the first pair of legs, the second and third pairs have coxae which articulate with the pleuron at two points. Their movement is thus more restricted. A small invagination of the lateral rim of the *mesocoxa*

forms a socket into which the coxal process fits; in addition, a rather broad *trochantin* (*TNII*) articulates medially with the anterior margin of the coxa and laterally with an anterior extension of the coxal process. Three tendons in the *pericoxal membrane* (*PEII*) provide insertions for muscles; *Tendon 40* lies just beside the medial end of the trochantin and is partially attached to the latter, *Tendon 41* is located in the posterior region of the pericoxal membrane, and *Tendon 42* lies just anterior and medial to the coxal process.

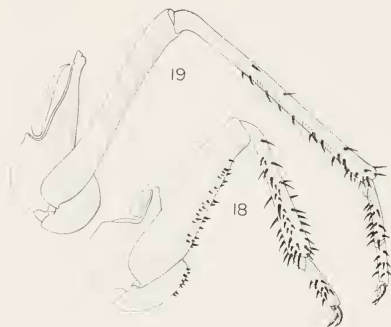


Figure 18. Medial view of the left mesothoracic leg and trochantin.

Figure 19. Medial view of the left metathoracic leg and trochantin.

The mesothoracic coxae lie closer to the body than do those of the prothorax. They project posteromedially, nearly touching each other at the midline (Fig. 2). Distally they are nearly spherical in shape; proximally the side which contacts the coxal process is considerably longer than the opposite side. The *basicoxal suture* is not as marked as that of the prothorax. It seems to disappear medially, while laterally it separates off the very narrow *anterior* and *posterior basicoxites*.

The joints between the various segments of the leg are essentially the same as those of the prothoracic leg. Also the tendons within the segments occupy the same positions as those of the

first pair of legs, their terminology and the corresponding prothoracic tendons being as follows: *Tendon 46* (Tendon 20), *Tendon 50* (Tendon 24), *Tendon 52* (Tendon 26), *Tendon 53* (Tendon 27), *Tendon 54* (Tendon 28), *Tendon 55* (Tendon 29).

The mesothoracic *femur* is longer and not nearly as broad as that of the prothorax, and it lacks the flattened ventral area. The *tibia* is also longer, and the *tarsus* consists of two segments, the first one being much reduced. The *unguitractor* of the *pretarsus* resembles that of the forelegs, and possesses similar terminal spines; the pretarsal *claws* are smaller than those of the first pair of legs. On the ventral surfaces of the *trochanter* and *femur* are rows of short spines. The *tibia* possesses longer spines on all its surfaces; these are especially numerous distally. A few spines are also present on the distal segment of the *tarsus*.

Metathoracic legs (Figs. 15 and 19). The metathoracic *coxae*, like those of the preceding segment, project posteromedially; distally they are very spherical, while proximally the side which contacts the coxal process is much elongated. They are articulated with the pleuron both directly, at the coxal process, and indirectly, by means of the very long *trochantin* (TNIII). Unlike the *coxae* of the two anterior pairs of legs, the metathoracic *coxa* forms a narrow lateral process at its rim, this process fitting into a socket on the coxal process; in the prothorax and mesothorax, the socket is on the *coxa*. The *pericoxal membrane* (PEIII) possesses only two tendons: *Tendon 63*, which is partially attached to the medial end of the *trochantin*, and *Tendon 64*, in the posterior part of the membrane. At the proximal end of the *coxa*, the *basicostal suture* separates off a distinct *posterior basicoxite* and a very narrow *anterior basicoxite*.

The form of the various joints and tendons is the same as in the first pair of legs. The terminology of the different tendons is as follows: *Tendon 70* (Tendon 20), *Tendon 74* (Tendon 24), *Tendon 76* (Tendon 26), *Tendon 77* (Tendon 27), *Tendon 78* (Tendon 28), and *Tendon 79* (Tendon 29).

The shapes of the *femur*, *tibia* and *tarsus* are quite different from those of the corresponding segments of the forelegs. Since the latter are modified for catching prey, while the former are adapted for jumping, these differences are not surprising. The

metathoracic femur is much longer and narrower than the prothoracic one. In the Hemiptera, according to Weber (1930), the main muscles of the jumping legs are those of the *trochanter*, not those of the tibia as in Orthoptera. In the gelastocorid foreleg, on the other hand, the tibial muscles are greatly developed for capturing prey, and therefore the femora, on which these muscles originate, are much enlarged. The metathoracic tibia and tarsus are also much longer than those of the foreleg, and the tarsus is three-segmented, the proximal segment being reduced. The great length of the femur, tibia, and tarsus provides additional leverage for jumping.

On the femur there are a few very fine spines or hairs, but very stout spines are present only on the tibia and tarsus, where they are very numerous. In addition, the ventral surfaces of the tibia and tarsus bear rows of long, fine hairs; there are two such rows on the tibia and one on the tarsus. Weber (1930) has suggested that the spines on the last two pairs of legs in gelastocorids help to anchor the legs in the sand and to prevent them from slipping backwards when the animal is jumping. The metathoracic tibial and tarsal hairs are probably used to clean the sides of the abdomen; the author has often observed live gelastocorids rubbing their hindlegs over the edges of the abdomen.

WINGS

Forewing. Most of the forewing is coriaceous, and its surface is covered with tubercles of various sizes, similar to those on the body. Its tip, the *membrane* (*MB*), is smooth-textured and less coriaceous. The rest of the wing is divided into *clavus* (*CV*), *corium* (*CO*), and *embolium* (*EM*), as shown in Figure 20. The boundaries between these areas are marked by very narrow membranous clefts in the surface of the wing. These probably represent wing veins, but the author will not attempt to homologize them. Both Tanaka (1926) and Hoke (1926) studied the veins of the forewings of a few Heteroptera, but none of the species studied by them resembles *Gelastocoris* closely enough to permit comparison. The boundary between the clavus and the corium is very clear, and the wing possesses a flexible fold along this line. The embolium is marked off by a long longitudinal and a short

transverse vein; these two do not meet medially. A fourth vein runs longitudinally along the middle of the clavus; it is difficult to see in many specimens.

The anterolateral edge of the embolium is greatly thickened and folded ventrally. In this thickened, folded region there is a large, socket-like depression which receives the knob on the posterolateral margin of the mesothoracic epimeron, holding the resting wing securely in place. Similar wing-locking devices have been reported in a great many Heteroptera by many authors,

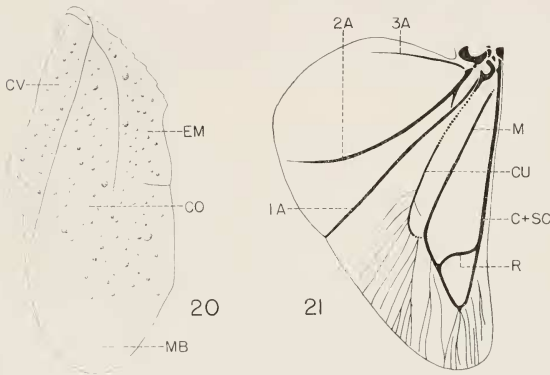


Figure 20. Dorsal view of the right forewing.

Figure 21. Dorsal view of the right hindwing.

and appear to be a common feature in this order of insects. As has been previously mentioned, the pleural sclerites ventral to the base of the forewing are somewhat evaginated, forming a shelf-like projection. The thickened edge of the embolium lies upon this shelf when the wing is at rest.

The axillary sclerites by which the forewing articulates with the mesothorax are shown in Figure 9. The *first axillary sclerite* (1AX), which articulates with the anterior notal wing process, is small and oval in shape; laterally it contacts a large, irregularly shaped *second axillary sclerite* (2AX). The latter is fused

anteriorly with the *humeral plate* (*H*), the boundary between the two being indistinct. A U-shaped *third axillary sclerite* (*3AX*) articulates anterolaterally with the posterior part of the second sclerite; posteromedially it is movably joined with a small *fourth axillary sclerite* (*4AX*). A suture divides this fourth sclerite into a proximal and a distal part, the proximal part articulating medially with the subalare. Lateral to the anterolateral portion of the third axillary sclerite is a small, triangular *median plate* (*MP*). This sclerite articulates anteriorly with a larger process (*MP?*) which appears to be the lateral part of the second axillary sclerite, but which may represent a second median plate which has become fused with that sclerite. A similar situation is found in the forewings of the belostomatids *Benacus* and *Lethocerus*; both Snodgrass (1909) and Lauck (1959), who studied these forms, considered the process in question to be a median plate.

Hindwing. Figure 21 shows the veins of the hindwing of *Gelastocoris*. For convenience, the homologies suggested by Hoke (1926) are used here. That author, who studied the wing venation of representatives of 25 families of Heteroptera, figured the hindwing of *Gelastocoris* sp.

As shown in Figure 9, the *first axillary sclerite* (*1AX*) of the hindwing articulates with the anterior notal wing process of the metathorax and is very small. The *third axillary sclerite* (*3AX*) is much larger and articulates with the posterior notal wing process; Taylor (1918) mistook it, in *Belostoma*, for the subalare. The third axillary sclerite is broad and U-shaped, bearing a small, knob-like projection laterally. This projection contacts the base of the *second anal vein* (Fig. 21, *2A*). Between the first and third sclerites lies a small *second axillary sclerite* (*2AX*); an even smaller, triangular *median plate* (*MP*) is located just lateral to the second axillary sclerite.

MUSCULATURE

In general, the names of the following muscles and the numbers by which they are designated are the same as those used by Larsén (1945a). A few of the muscles described by Larsén appear to consist of two parts in *Gelastocoris*; in such cases they

have been given the name proposed by that author, with the addition of "primus" or "secundus", and an "A" or "B" has been added to Larsén's number. All the thoracic muscles are paired.

An attempt has been made to list, for each muscle, similar muscles which have been reported in other Heteroptera. Those listed are included because both their origins and their insertions, as described in the literature, are the same or very similar to those of the corresponding muscle in *Gelastocoris*. Whether or not they are actually homologous to the gelastocorid muscle which they resemble cannot, in most cases, be definitely stated. The names used by Larsén are given only when they differ from those employed in the current work.

In Figures 22-31, the muscles are designated by the numbers given below.

MUSCLES OF THE PROTHORAX

1. M. PRONOTI PRIMUS (Fig. 22)

Origin: Anteromedial region of the pronotum.

Insertion: On the two tendons in the mid-dorsal region of the cervical membrane.

Action: Raises and retracts the head.

2. M. PRONOTI SECUNDUS (Fig. 22)

Origin: Anterior region of the pronotum, lateral to *M. pronoti primus*.

Insertion: Tip of the occipital condyle.

Action: Rotates or depresses the head.

Similar muscles: Muscle 1 and Muscle 2 (?) (Malouf, 1933); cephalic depressor (?) (Rawat, 1939); first and second pairs of levators of head (Akbar, 1957).

3. M. PRONOTI TERTIUS (Fig. 22)

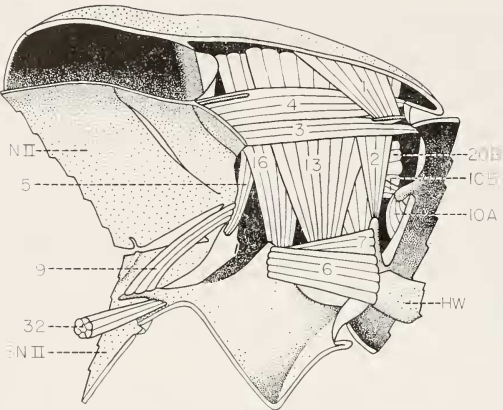
A well developed longitudinal muscle.

Origin: Ventral part of the first phragma.

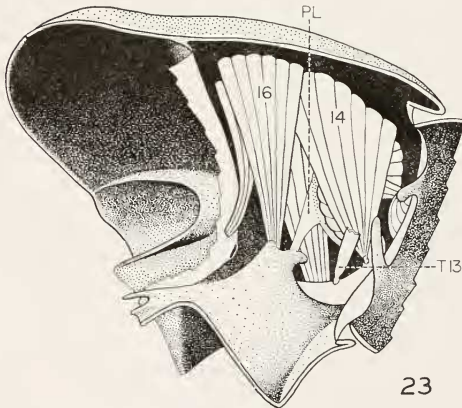
Insertion: On the dorsomedial margin of the postocciput, and on the two tendons in the cervical membrane.

Action: Raises and retracts the head.

Similar muscles: Tergal longitudinal muscle (Malouf, 1933); ventral fibers of dorsal muscle (Rawat, 1939); indirect levators of head (Akbar, 1957).



22



23

Figure 22. Medial view of the left half of the prothorax showing the more medial muscles. The left halves of the postocciput and of the anterior part of the mesothorax are shown in place.

Figure 23. Same view as above. The mesothorax and Muscles 1, 2, 3, 4, 6, 7, 9, and 13 have been removed. Tendon 13 has been cut off near its base.

4. *M. PRNOTI QUARTUS* (Fig. 22)
A well developed longitudinal muscle, just dorsal to *M. pronoti tertius*.
Origin: On the dorsal part of the first phragma, and on the two tendons in the intersegmental membrane.
Insertion: On the inturned dorsomedial margin of the pronotum.
Action: Raises the prothorax.
Similar muscles: Muscle rétracteur du prothorax (Poisson, 1924); dorsal fibers of dorsal muscle (Rawat, 1939).
5. *M. PRNOTI QUINTUS* (Fig. 22)
A slender muscle.
Origin: On the small sclerite in the intersegmental membrane anterior to the prealar bridge of the mesothorax.
Insertion: Posterior region of the pronotum.
Action: Depresses the prothorax.
Similar Muscles: Indirect protractor of fore legs (Malouf, 1933); depressors of pronotum (?) (Akbar, 1957).
6. *M. PROSTERNI PRIMUS* (Fig. 22)
A broad longitudinal muscle.
Origin: Anterior surface of the medial arm of the prothoracic furca.
Insertion: On the occipital condyle and on the tip of the hypopharyngeal wing.
Action: Depresses and retracts the head. May also cause some rotation.
Similar muscles: Sternal longitudinal muscle (Malouf, 1933); depresso-extensors of head (Akbar, 1957).
7. *M. PROSTERNI SECUNDUS* (Fig. 22)
A broad longitudinal muscle, just lateral to *M. prosterni primus*.
Origin: Anterior surface of the lateral arm of the prothoracic furca.
Insertion: Occipital condyle.
Action: Same as *M. prosterni primus*.
9. *M. DORSOVENTRALIS* (Fig. 22)
A slender muscle.
Origin: Anterior margin of the prealar bridge of the mesothorax, medial to *M. pronoti quintus*.
Insertion: Posterior sternal process of the prothorax.
Action: Raises the posterior part of the prosternum, thus depressing the prothorax as a whole.
Similar muscles: Tergo-sternal fureal muscle (Rawat, 1939); fu₁-prsc₂ (Lauck, 1959).

- 10A. *M. PROEPISTERNO-POSTOCCIPITALIS PRIMUS* (Fig. 22)
A short muscle.
Origin: Anterolateral region of the proepisternum.
Insertion: Lateral apodeme of the postoccipt.
Action: Raises the head (contraction of both muscles) or moves it to one side (contraction of one muscle).
Similar muscles: Part of *M. proepisterno-postooccipitalis* (Larsén, 1945a); promotio-extensors of head (?) (Akbar, 1957).
- 10B. *M. PROEPISTERNO-POSTOCCIPITALIS SECUNDUS* (Figs. 22 and 24)
A short muscle.
Origin: Lateral surface of the prothoracic pleural apophysis.
Insertion: Tip of the lateral apodeme of the postoccipt.
Action: Depresses the head (contraction of both muscles) or moves it to one side (contraction of one muscle).
Similar muscle: Part of *M. proepisterno-postooccipitalis* (Larsén, 1945a).
13. *M. NOTO-TROCHANTINALIS* (Fig. 22)
A large, fan-shaped muscle.
Origin: Pronotum, just lateral to *M. pronoti primus*.
Insertion: Tendon 13, at the medial end of the trochantin.
Action: Rotates the coxa and promotes the leg.
Similar muscles: Tergal promotor of coxa (?) (Malouf, 1933); tergal promotor (Rawat, 1939); first promotor of coxa (?) (Akbar, 1957).
14. *M. NOTO-COXALIS PRIMUS* (Fig. 23)
A large, fan-shaped muscle.
Origin: Pronotum, lateral to *M. pronoti secundus* and *M. noto-trochantinalis*.
Insertion: Tendon 14, lateral to the trochantin.
Action: Rotates the coxa and abducts the leg.
Similar muscles: Internal rotator (Rawat, 1939); second promotor of coxa (?) (Akbar, 1957).
15. *M. NOTO-COXALIS SECUNDUS* (Fig. 25)
A large, fan-shaped muscle.
Origin: Posterolateral region of the pronotum.
Insertion: Tendon 15, just posterior to the coxal process.
Action: Rotates the coxa and remotes the leg.
Similar muscles: External rotator (Rawat, 1939); first remotor of coxa (?) (Akbar, 1957).

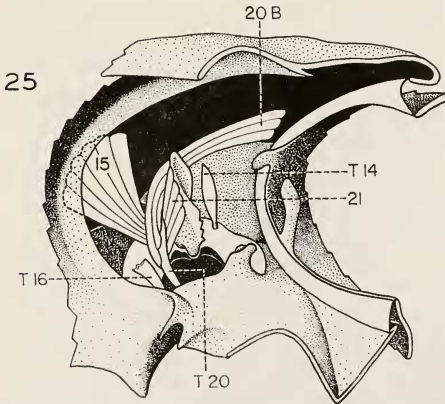
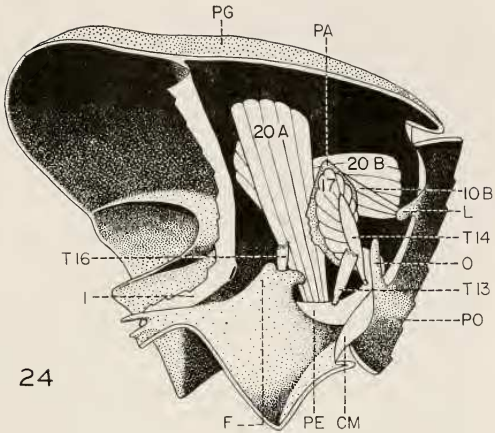


Figure 24. Same view as Fig. 22. Muscles 5, 10A, 14, and 16 have been removed. Tendon 16 has been cut off near its base, and the pleurosternal bridge has been cut away.

Figure 25. Posteromedial view of the left half of the prothorax and of the postcoeciput (same view as Fig. 5), showing Muscles 15, 20B, and 21. The posterior lobes of the pronotum and epimeron have been cut away, and the pleurosternal bridge has been removed.

16. M. NOTO-COXALIS TERTIUS (Figs. 22 and 23)
A large, fan-shaped muscle.
Origin: Pronotum, posterior and lateral to *M. noto-trochantinalis*.
Insertion: Tendon 16, in the posteromedial region of the pericoxal membrane.
Action: Rotates the coxa and adducts the leg.
Similar muscles: Tergal remotor of coxa (?) (Malouf, 1933); tergal remotor (Rawat, 1939).
17. M. PLEURA-COXALIS (Fig. 24)
A short, broad muscle.
Origin: Medial surface of the prothoracic pleural apophysis.
Insertion: Tendon 14.
Action: Same as *M. noto-coxalis primus*.
- 20A. M. NOTO-TROCHANTERALIS PRIMUS (Fig. 24)
A long, well-developed muscle.
Origin: Pronotum, between *M. noto-coxalis secundus* and *M. noto-coxalis tertius*.
Insertion: Tendon 20, from the part of the proximal rim of the trochanter which is farthest from the femur.
Action: Depresses the trochanter.
Similar muscles: Depressor of trochanter, tergal branch (Malouf, 1933); extra-coxal depressor, branch from tergum (Rawat, 1939); part of *M. noto-trochanteralis* (Larsén, 1945a); tergal depressor of trochanter (Akbar, 1957).
- 20B. M. NOTO-TROCHANTERALIS SECUNDUS (Figs. 22, 24, and 25)
A long, slender muscle.
Origin: Anterolateral region of the pronotum, very near the lateral margin of the episternum.
Insertion: Tendon 20.
Action: Depresses the trochanter.
Similar muscles: Extra-coxal depressor, branch from tergum (?) (Rawat, 1939); part of *M. noto-trochanteralis* (Larsén, 1945a).
21. M. PLEURA-TROCHANTERALIS (Fig. 25)
A short, broad muscle.
Origin: Lateral surface of the prothoracic apophysis.
Insertion: Tendon 20.
Action: Depresses the trochanter.
Similar muscles: Depressor of trochanter, pleural branch (Malouf, 1933); extra-coxal depressor, branch from pleural region (Rawat, 1939); pleural depressor of trochanter (?) (Akbar, 1957).

MUSCLES OF THE MESOTHORAX

30. M. MESONOTI PRIMUS (Fig. 26)

When developed, this is the largest muscle in the thorax. In the majority of specimens, however, it, like the other indirect flight muscles, is degenerate.

Origin: Anterior surfaces of the medial part of the second phragma and of the ventral processes of the latter.

Insertion: First phragma and prescutum of the mesothorax.

Action: Indirect flight muscle. Depresses the forewing by acting in antagonism to *M. dorsoventralis primus* and *M. mesonoti secundus*.

Similar muscles: Muscle vibrateur dorsal longitudinal (Poisson, 1924); tergal longitudinal muscle (Malouf, 1933); dorsal muscles of mesothorax (Rawat, 1939); indirect and principal depressor of fore-wings (Akbar, 1957); 1ph-2ph and sc2-2ph (Lauck, 1959).

31. M. MESONOTI SECUNDUS (Figs. 26 and 27)

Quite large when developed; degenerate in the majority of specimens.

Origin: Lateral surface of the ventral process of the second phragma.

Insertion: Anterolateral region of the mesoscutum.

Action: Indirect flight muscle, raising the forewings. Its contraction forces the anterior notal wing process downward upon the first axillary sclerite. Since the pleural wing process forms a fulcrum upon which the second axillary sclerite pivots, the rest of the wing is forced upwards.

Similar muscles: Tergal longitudinal oblique muscle (Malouf, 1933); secondary indirect levator of fore-wings (Akbar, 1957); sc-scl2-2ph (Lauck, 1959).

32. M. MESOSTERNI PRIMUS (Figs. 22 and 26)

A fairly long, well-developed muscle.

Origin: Anterior surface of the mesothoracic furca.

Insertion: Posterior part of the prosternum, between the posterior sternal processes.

Action: Depresses the prothorax.

Similar muscles: Sternal longitudinal muscle (?) (Malouf, 1933); ventral muscle of mesothorax (Rawat, 1939); fu₁-fu₂ (Lauck, 1959).

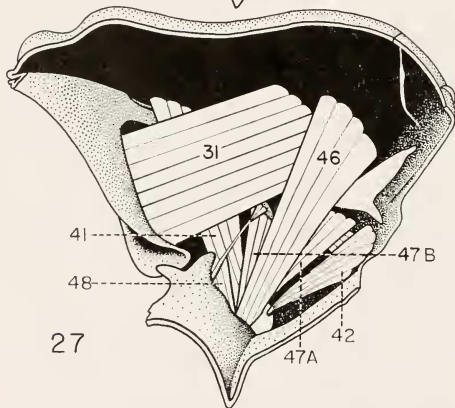
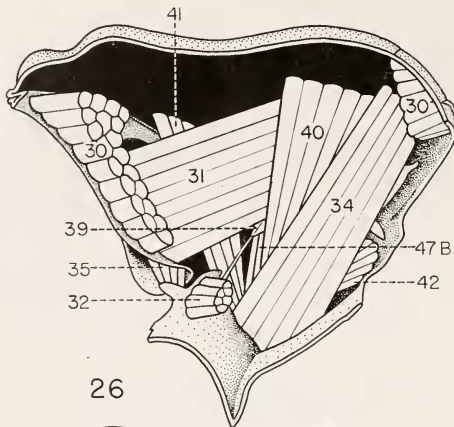


Figure 26. Medial view of the left half of the mesothorax (same view as Fig. 12 *t*, showing the more medial mesothoracic muscles. The middle part of Muscle 30 has been cut away. Muscles 30, 31, and 34 are fully developed in this specimen.

Figure 27. Same view as above. Muscles 30, 32, 34, 35, and 40 have been removed. Tendon 40 is not shown.

34. *M. DORSOVENTRALIS PRIMUS* (Fig. 26)
Large when developed; degenerate in the majority of specimens.
Origin: In a depression on the mesothoracic precoxal bridge, just anterior to the coxal cavity.
Insertion: Anterior part of the mesoscutum, just lateral to the parapsidal ridge.
Action: Same as *M. mesonoti secundus*.
Similar muscles: Muscle vibrateur transversal (sternali-dorsal) (Poisson, 1924); tergo-sternal muscle (Malouf, 1933); indirect and principal levator of fore-wings (Akbar, 1957); sc_2-bs_2 (Lauck, 1959).
35. *M. DORSOVENTRALIS SECUNDUS* (Fig. 26)
A very short muscle.
Origin: Posterior arm of the mesothoracic furca.
Insertion: Tip of the ventral process of the second phragma, between the two layers of this process.
Action: Depresses the posterior mesotergum and the anterior metatergum (?).
Similar muscles: Tergo-sterno-furcal muscle (Malouf, 1933); tergo-sternal furcal muscle of mesothorax (Rawat, 1939); secondary indirect depressor of fore-wings (Akbar, 1957); $2ph-fu_2$ (Lauck, 1959).
38. *M. EPISTERNO-ALARIS* (Fig. 30)
Lies beneath *M. pleura-trochanteralis primus* and *M. episterno-coxalis*.
Origin: Anterior region of the mesothoracic episternum, just posterior to the point of origin of *M. episterno-coxalis*.
Insertion: On a tendon from the "elbow" of the third axillary sclerite of the forewing.
Action: Direct flight muscle. Contraction causes the third axillary sclerite to flip over, thus flexing a previously extended forewing.
Similar muscles: First flexor of fore wing (Malouf, 1933; Akbar, 1957); axillary muscle of mesothorax (Rawat, 1939); $3ax_2-eps_2$ (Lauck, 1959).
39. *M. FURCA-PLEURALIS* (Figs. 26 and 30)
A very minute muscle.
Origin: Tip of the mesothoracic furcal apodeme.
Insertion: Tip of the mesothoracic pleural apophysis.
Action: Uncertain.
Similar muscles: Sterno-pleuro-apophysal muscle (Malouf, 1933); pleurosternal muscle (Rawat, 1939); promotio-extensor of fore-wings (?) (Akbar, 1957); plr_2-fu_2 (Lauck, 1959).

40. M. NOTO-TROCHANTINALIS (Fig. 26)
 A well-developed, fan-shaped muscle.
Origin: Mesoseutum, between *M. dorsoventralis primus* and *M. noto-trochanteralis*.
Insertion: Tendon 40, at the medial end of the mesothoracic trochantin.
Action: Rotates the coxa and promotes the leg.
Similar muscles: Tergal promotor of coxa (Malouf, 1933); tergal promotor of mesothorax (Rawat, 1939); *se-scl₂-ex₂* (Lauck, 1959).
41. M. NOTO-COXALIS (Figs. 26, 27, and 30)
 A well-developed, fan-shaped muscle.
Origin: Posterolateral limit of the mesoseutum.
Insertion: Tendon 41, in the posterior region of the pericoxal membrane.
Action: Rotates the coxa and remotes the leg.
Similar muscles: Tergal remotor of coxa (Malouf, 1933); tergal remotor of mesothorax (Rawat, 1939); first remotor of coxa (Akbar, 1957); *se-scl₂'-ex₂'* (Lauck, 1959).
42. M. EPISTERNO-COXALIS (Figs. 26, 27, and 30)
 A rather small, fan-shaped muscle.
Origin: Anterior part of the mesothoracic episternum, in the region of the prealar bridge.
Insertion: Tendon 42, just anterior to the coxal process.
Action: Rotates the coxa and promotes the leg.
Similar muscles: Sternal promotor of coxa (?) (Malouf, 1933); second promotor of coxa (Akbar, 1957); *eps₂-ex₂* (Lauck, 1959).
46. M. NOTO-TROCHANTERALIS (Fig. 27)
 A well-developed muscle.
Origin: Mesoscutum, between *M. mesonoti secundus* and *M. noto-trochantinalis*.
Insertion: Tendon 46, from the part of the proximal rim of the trochanter which is farthest from the femur.
Action: Depresses the trochanter.
Similar muscles: Depressor of telopodite, tergal branch (Malouf, 1933); extra-coxal depressor of the trochanter of the mesothorax, tergal branch (Rawat, 1939); tergal depressor of trochanter (Akbar, 1957); *se-scl₂-tr₂* (Lauck, 1959).

- 47A. *M. PLEURA-TROCHANTERALIS PRIMUS* (Figs. 27 and 30)
 A rather slender muscle.
Origin: Anterior part of the mesothoracic episternum, just lateral to *M. episterno-coxalis*.
Insertion: Tendon 46.
Action: Depresses the trochanter.
Similar muscles: Depressor of telopodite, pleural branch (Malouf, 1933); extra-coxal depressor of the trochanter of the mesothorax, pleural branch (Rawat, 1939); part of *M. pleura-trochanteralis* (Larsén, 1945a); pleural depressor of trochanter (Akbar, 1957); eps₂-tr₂ (Lauck, 1959).
- 47B. *M. PLEURA-TROCHANTERALIS SECUNDUS* (Figs. 26, 27, and 30)
Origin: Medial surface of the mesothoracic pleural apophysis.
Insertion: Tendon 46.
Action: Depresses the trochanter.
Similar muscles: Extra-coxal depressor of the trochanter of the mesothorax, pleural branch (Rawat, 1939); part of *M. pleura-trochanteralis* (Larsén, 1945a).
48. *M. FURCA-TROCHANTERALIS* (Figs. 27 and 30)
 A small muscle, rather difficult to see.
Origin: Base of the furcal apodeme of the mesothorax.
Insertion: Tendon 46.
Action: Depresses the trochanter.
Similar muscles: Extra-coxal depressor of the trochanter of the mesothorax, sternal branch (Rawat, 1939); fu₂-tr₂ (Lauck, 1959).

MUSCLES OF THE METATHORAX

60. *M. DORSOVENTRALIS* (Fig. 28)
 A slender muscle.
Origin: Tip of the metathoracic furca.
Insertion: Third phragma, lateral to the midline.
Action: Depresses the posterior part of the metanotum (?).
Similar muscles: Tergo-sternal furcal muscle of metathorax (Rawat, 1939); 3ph-fu₃ (Lauck, 1959).
61. *M. EPISTERNO-ALARIS* (Figs. 29 and 30)
 A very slender muscle, difficult to see.
Origin: Lateral part of the metathoracic episternum, just lateral to the point of origin of *M. pleura-trochanteralis*.
Insertion: On a tendon from the "elbow" of the third axillary sclerite of the hindwing.

Action: Direct flight muscle. Flexes the hindwing in the same way that *M. episterno-alaris* of the mesothorax flexes the forewing.

Similar muscles: Flexor of hind wing (Malouf, 1933); axillary muscle of metathorax (Rawat, 1939); first flexor of hindwings (Akbar, 1957); 3ax-eps₃ (Lauek, 1959).

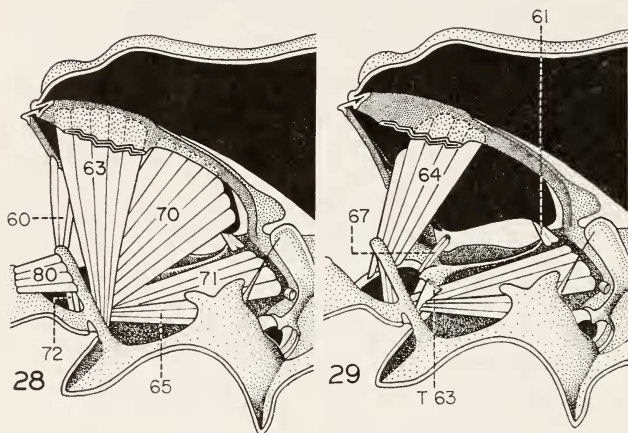


Figure 28. Medial view of the left halves of the metathorax and of the posterior mesothorax (same view as Fig. 12), showing the more medial metathoracic and abdominal muscles. The ventral process of the second phragma has been cut off.

Figure 29. Same view as above. Muscles 60, 63, 70, and 80 have been removed.

63. *M. NOTO-TROCHANTINALIS* (Fig. 28)

A well-developed, fan-shaped muscle.

Origin: Anterior part of the metanotum, just lateral to the midline.

Insertion: Tendon 63, at the medial end of the metathoracic trochantin.

Action: Rotates the coxa and promotes the leg.

Similar muscles: Tergal promotor of coxa (Malouf, 1933); tergal promotor of metathorax (Rawat, 1939); first promotor of coxa (?) (Akbar, 1957); sc₂-ex₃ (Lauek, 1959).

64. *M. NOTO-COXALIS* (Figs. 29 and 30).

A well-developed, fan-shaped muscle.

Origin: Metanotum, lateral and posterior to *M. noto-trochantinalis*.

Insertion: Tendon 64, in the posterior part of the pericoxal membrane.

Action: Rotates the coxa and remotes the leg.

Similar muscles: Tergal remotor of coxa, first branch (Malouf, 1933); tergal remotor of metathorax (Rawat, 1939); first remotor of coxa (Akbar, 1957); sc_3' - cx_3' (Lauck, 1959).

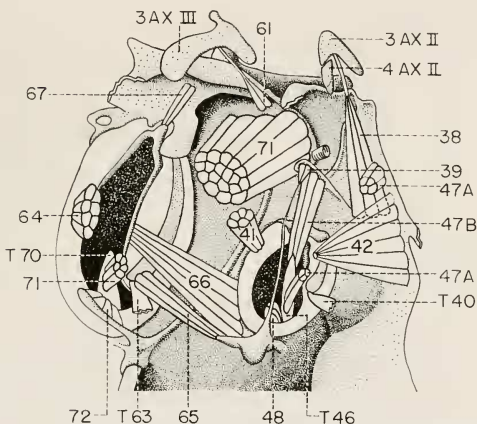


Figure 30. Dorsal view of the inner ventral surface of the pterothorax, left side (same view as Fig. 15), showing the ventral and lateral muscles. The middle parts of Muscles 47A and 71 have been cut away, and most of the tendons of the leg muscles, along with Muscles 41 and 64, have been cut off near their bases. The third and fourth axillary sclerites are shown in place.

65. *M. FURCA-TROCHANTINALIS* (Figs. 28 and 30)

A slender muscle, rather difficult to see.

Origin: Base of the posterior arm of the mesothoracic furca.

Insertion: On Tendon 63 and on the medial end of the metathoracic trochantin.

Action: Rotates the coxa and promotes the leg.

Similar muscle: *M. episterno-trochantinalis* (?) (Larsén, 1945a).

66. M. EPISTERNO-COXALIS (Fig. 30)
A flat, broad muscle lateral to *M. furca-trochantinalis*.
Origin: On the ridge bordering the posterior margin of the mesothoracic coxal cavity (Larsén, 1945a, considered this ridge to be part of the metathoracic episternum).
Insertion: Anterior margin of the anterior basicoxite of the metathoracic coxa.
Action: Rotates the coxa and promotes the leg.
Similar muscle: Sternal promotor of metathorax (?) (Rawat, 1939).
67. M. COXA-SUBALARIS (Figs. 29 and 30)
A slender muscle.
Origin: On the basicostal suture of the metathoracic coxa, in the region of the coxal process.
Insertion: On the very small metathoracic subalare.
Action: Direct flight muscle. Depresses the posterior margin of the hindwing.
Similar muscles: Depressor of posterior margin of hind wing (Malouf, 1933); second flexor of hind-wings (Akbar, 1957).
70. M. NOTO-TROCHANTERALIS (Fig. 28)
A very well-developed muscle.
Origin: Lateral part of the metanotum.
Insertion: Tendon 70, from the part of the proximal rim of the trochanter which is farthest from the femur.
Action: Depresses the trochanter.
Similar muscles: Depressor of trochanter, tergal branch (Malouf, 1933); extra-coxal depressor of the trochanter of the metathorax, tergal branch (Rawat, 1939); tergal depressor of trochanter (Akbar, 1957); sc₃-tr₃ (Lauck, 1959).
71. M. PLEURA-TROCHANTERALIS (Figs. 28 and 30)
A very well-developed muscle.
Origin: Lateral and anterolateral region of the metathoracic episternum.
Insertion: Tendon 70.
Action: Depresses the trochanter.
Similar muscles: Depressor of trochanter, pleural branch (Malouf, 1933); extra-coxal depressor of the trochanter of the metathorax, pleural branch (Rawat, 1939); pleural depressor of trochanter, (Akbar, 1957).
72. M. FURCA-TROCHANTERALIS (Figs. 28 and 30)
Origin: Base of the metathoracic furca.
Insertion: Tendon 70.

Action: Depresses the trochanter.

Similar muscles: Extra-coxal depressor of the trochanter of the metathorax, sternal branch (Rawat, 1939); fu₃-tr₃ (Lauck, 1959).

80. M. VENTRALIS ABDOMINALIS (Fig. 28)

A short, broad abdominal muscle.

Origin: Posterior surface of the metathoracic furca.

Insertion: On a ridge on the ventrolateral part of the second abdominal segment.

Action: Raises the abdomen.

Similar muscles: veM₁ (Larsén, 1945a); fu₃-2S (Lauck, 1959).

INTRINSIC MUSCLES OF THE LEGS

Prothoracic legs (Fig. 31)

23. M. COXA-TROCHANTERALIS MEDIALIS

A short, broad, well-developed muscle.

Origin: Posteromedial wall of the coxa.

Insertion: Tendon 20.

Action: Depresses the trochanter.

Similar muscles: Coxal branch of depressor of trochanter (Malouf, 1933); depressor of the trochanter (Rawat, 1939); coxal depressor of trochanter (Akbar, 1957).

24. M. COXA-TROCHANTERALIS LATERALIS

A muscle consisting of three bundles.

Origin: Anterior wall of the coxa.

Insertion: On the three-branched Tendon 24, from the part of the proximal rim of the trochanter which is nearest the femur.

Action: Raises the trochanter.

Similar muscles: Levator of trochanter (as shown in Pl. XVI, fig. 1, by Malouf, 1933; Rawat, 1939; Akbar, 1957).

25. M. REDUCTOR FEMORIS

A short, broad muscle.

Origin: Posteromedial wall of the trochanter.

Insertion: Lateral part of the proximal margin of the femur. Some strands enter the femur and insert on Tendon 26.

Action: Moves femur laterally. Strands entering the femur depress the tibia.

Similar muscles: Remotor of femur (Malouf, 1933); reductor of the femur (Rawat, 1939; Akbar, 1957).

26. M. DEPRESSOR TIBIAE

A very well-developed muscle.

Origin: Walls of the ventral half of the femur.

Insertion: Tendon 26, from the ventral region of the proximal margin of the tibia.

Action: Depresses the tibia, closing it upon the femur.

Similar muscles: Depressor of tibia (Malouf, 1933; Rawat, 1939; Akbar, 1957).

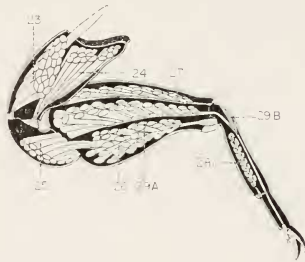


Figure 31. Medial view of the left prothoracic leg, with the medial walls of the leg removed (same view as Fig. 17), showing the intrinsic leg muscles.

27. M. LEVATOR TIBIAE

Less well-developed than *M. depressor tibiae*.

Origin: Walls of the most dorsal part of the femur.

Insertion: Tendon 27, from the dorsal region of the proximal margin of the tibia.

Action: Raises the tibia.

Similar muscles: Levator of tibia (Malouf, 1933; Rawat, 1957); extensor of tibia (Akbar, 1957).

28. M. DEPRESSOR TARSII

Composed of many short, fine muscle strands.

Origin: Ventrolateral walls of the tibia.

Insertion: Tendon 28, from the ventral region of the proximal margin of the tarsus.

Action: Depresses the tarsus.

Similar muscles: Depressor of tarsus (Malouf, 1933; Rawat, 1939; Akbar, 1957).

29A. M. DEPRESSOR PRAETARSI PRIMUS

A well-developed muscle.

Origin: Lateral walls of the dorsal half of the femur, between *M. depressor tibiae* and *M. levator tibiae*.

Insertion: Intrafemoral part of Tendon 29, from the unguitactor of the pretarsus.

Action: Depresses the pretarsus.

Similar muscles: Depressor of pretarsus, femoral branch (Malouf, 1933; Rawat, 1939); part of *M. depressor praetarsi* (Larsén, 1945a); depressor of pretarsus, proximal muscle (Akbar, 1957).

29B. M. DEPRESSOR PRAETARSI SECUNDUS

A very weak muscle, consisting of only a few strands.

Origin: Proximal region of the dorsal wall of the tibia.

Insertion: Intratibial part of Tendon 29.

Action: Depresses the pretarsus.

Similar muscles: Depressor of pretarsus, tibial branch (Malouf, 1933; Rawat, 1939); part of *M. depressor praetarsi* (Larsén, 1945a); depressor of pretarsus, distal muscle (Akbar, 1957).

Pterothoracic legs

Each of the following muscles (Nos. 49-55B and Nos. 73-79B) corresponds to a similar muscle in the foreleg which bears the same name. The origins, insertions, and actions of the corresponding muscles are similar, and each muscle, with the exception of *M. coxa-trochanteralis medialis*, inserts on a tendon bearing the same number as the muscle. In the following account, for each pterothoracic muscle the number of the corresponding prothoracic muscle will be noted, along with any significant differences in general appearance.

Mesothoracic legs

49. M. COXA-TROCHANTERALIS MEDIALIS

Similar to Muscle 23. Inserts on Tendon 46.

50. M. COXA-TROCHANTERALIS LATERALIS

Similar to Muscle 24.

51. M. REDUCTOR FEMORIS

Similar to Muscle 25.

52. M. DEPRESSOR TIBIAE

Similar to Muscle 26, but less well developed.

53. M. LEVATOR TIBIAE

Similar to Muscle 27, but somewhat less well developed.

54. M. DEPRESSOR TARSII
Similar to Muscle 28.
- 55A. M. DEPRESSOR PRAETARSII PRIMUS
Similar to Muscle 29A, but much less well developed.
- 55B. M. DEPRESSOR PRAETARSII SECUNDUS
Similar to Muscle 29B.

Metathoracic legs

73. M. COXA-TROCHANTERALIS MEDIALIS
Similar to Muscle 23. Inserts on Tendon 70.
74. M. COXA-TROCHANTERALIS LATERALIS
Similar to Muscle 24.
75. M. REDUCTOR FEMORIS
Similar to Muscle 25.
76. M. DEPRESSOR TIBIAE
Similar to Muscle 26, but much less well developed.
77. M. LEVATOR TIBIAE
Similar to Muscle 27, but less well developed.
78. M. DEPRESSOR TARSII
Similar to Muscle 28; the muscle strands are shorter and weaker.
- 79A. M. DEPRESSOR PRAETARSII PRIMUS
Similar to Muscle 29A, but much less well developed.
- 79B. M. DEPRESSOR PRAETARSII SECUNDUS
Similar to Muscle 29B.

DISCUSSION

Among the Heteroptera, degeneration of the flight muscles, such as has been observed in the large majority of the gelastocorids examined, is not uncommon. Many species have individuals which are unable to fly because of reduction of the wings, of the muscles, or of both. Polymorphism of the wings is found in some terrestrial families, such as the Pyrrhocoridae, Aradidae, and Lygaeidae (Weber, 1930) and in many aquatic and semi-aquatic families. Poisson (1924), who studied polymorphism in the aquatic Corixidae, Aphelocheiridae, and Naucoridae, and in the semi-aquatic Gerridae, Hydrometridae, Veliidae, and Mesovelidae, found that individuals with reduced wings usually showed degenerate flight muscles, although in a few cases the muscles were normal. Larsén (1950) found that in *Aphelocheirus* the degree

of reduction of the flight musculature increased in proportion to the amount of reduction of the wings.

Degeneration of the flight muscles in normal-winged individuals, as in *Gelastocoris*, is also quite common in both aquatic and terrestrial Heteroptera (Larsén, 1950). Among the aquatic forms, it has been reported in the Nepidae, Naucoridae, and Aphelocheiridae (Ferrière, 1914; Poisson, 1924; Larsén, 1949 and 1950). In their general appearance, the degenerate muscles of *Gelastocoris* closely resemble the reduced muscles of macrop-terous individuals of *Aphelocheirus*, as illustrated by Larsén (1950; his Fig. 8b). The degenerate dorsal longitudinal muscles of the mesothorax were termed the "tracheo-parenchymatous organ" by some authors because of the abundance of tracheoles which penetrate them. Early workers such as Dufour (1833) and Dogs (1909) believed this "organ" to be respiratory in function. It appears, however, that the tracheoles are only those which would penetrate a normal muscle, and that the tracheo-parenchymatous organ has no special respiratory function (Ferrière, 1914; Brocher, 1916). A degenerate *M. mesonoti primus* of *Gelastocoris*, when teased apart and examined under a compound microscope, shows a rich supply of tracheoles similar to those figured by Ferrière in the tracheo-parenchymatous organ of *Nepa*.

One puzzling feature noted in the present investigation is that although some gelastocorids possess well developed flight muscles as well as normal wings none of the insects were ever observed to fly. During nearly a year of captivity they were constantly given opportunities to do so, but never showed any inclination towards flight. Larsén (1950) made a similar observation on a few individuals of *Ranatra* which never flew even when strongly stimulated to do so. Examination of their musculature showed it to be normal. That author proposed that this might be due to a reduction of the nervous component of the flight apparatus. Whether or not this is a plausible explanation for the lack of flight in *Gelastocoris* may be elucidated by further anatomical work. Todd (1955), who also observed no flight in *Gelastocoris oculatus*, has noted that several other species of Gelastocoridae have forewings which are fused or which have reduced membranes, and in some species the hindwings are reduced.

The present study offers a few clues to the possible phylogenetic position of the Gelastocoridae among the Heteroptera. A brief review of the literature on this problem has been presented in a previous paper (Parsons, 1959), and the reader is referred to that work for a discussion of the theories of earlier authors. It is generally agreed that the three littoral families Gelastocoridae, Ochteridae, and Saldidae are closely related to each other, the first-named family having arisen from the second. It also appears that these three families represent a stage in the evolution of the totally aquatic and semi-aquatic bugs (the Hydrocorisae and Amphibicorisae respectively) from the terrestrial forms (the Geocorisae). Authorities have disagreed, however, as to which of the littoral families are related to the Hydrocorisae and which to the Amphibicorisae. De la Torre-Bueno (1923) believed the Hydrocorisae to be descended from saldid-like ancestors, with the ochterids and gelastocorids as intermediate stages. Spooner's (1938) work on the head capsule led him to place the latter two families with the Amphibicorisae, and the saldids with the Geocorisae. More recently, China (1955) has proposed that the Amphibicorisae arose from "Proto-Saldidae" and the Hydrocorisae from "Proto-Ochteridae."

Larsén (1945b), after studying a large number of heteropteran families, found five characteristics of the thoracic skeleton which seem to be more typical of the Hydrocorisae than of the other Heteroptera. First, the metanotum of the aquatic bugs is longer than the metapostnotum; in the Geocorisae the latter is longer than the former, while in *Salda* (Saldidae) the two are equal in length. Unfortunately, the boundary between these two regions is indistinct in the Amphibicorisae studied by Larsén, so that it is difficult to compare them with the Hydrocorisae and Geocorisae. The present study has shown the metanotum of *Gelastocoris* to be much longer than the metapostnotum, and in this character it resembles the Hydrocorisae.

A second feature of the Hydrocorisae, according to Larsén, is the presence, in all three thoracic segments, of a distinct pleural ridge (except in the mesothorax of *Ranatra*). Taylor (1918) also pointed out the distinctness of the pleural ridge in the pterothorax of corixids, belostomatids, and notonectids. In all the semi-aquatic and terrestrial bugs studied by Larsén, the pleural

ridge is indistinct in at least one segment. A distinct prothoracic pleural ridge with a pleural apophysis is present in all of the Hydrocorisae studied by Larsén, but in only three of the Geocorisae and in none of the Amphibicorisae. In *Gelastocoris*, however, all three segments show distinct pleural ridges, and a prothoracic pleural apophysis is present. A large posterior lobe on the mesothoracic epimeron is a third character distinguishing the Hydrocorisae. This lobe is quite extensive in *Gelastocoris*, overlapping much of the metathoracic episternum, and its size is comparable to that of the aquatic bugs *Hesperocorixa*, *Notonecta*, and *Pelocoris*. In the Amphibicorisae, in *Salda*, and in most of the Geocorisae studied by Larsén the posterior mesothoracic epimeral lobe is more weakly developed. Two other Geocorisae showing weakly developed mesothoracic epimeral lobes are *Nezara* (Malouf, 1933) and *Leptocoris*a (Akbar, 1957).

A fourth characteristic of the aquatic bugs, as cited by Larsén, concerns the width of the metathoracic epimeron which is not as reduced as in many terrestrial bugs. Unfortunately, he did not compare the width of this sclerite in the Amphibicorisae and the Hydrocorisae, and did not state how many, if any, Geocorisae are exceptions to this generalization. The metathoracic epimeron of *Gelastocoris* appears to be as well developed as that of the aquatic bugs *Hesperocorixa*, *Notonecta*, *Pelocoris*, *Belostoma*, *Nepa*, and *Ranatra*. Finally, Larsén stated that the mesothoracic pleural apophysis in the Hydrocorisae is large and extends dorsally. The size of this process in *Gelastocoris* is comparable to that of *Belostoma* and of *Naucoris* as figured by Larsén (1945a); it appears to be somewhat smaller than that of *Notonecta*, but is considerably larger than that of *Hesperocorixa* and *Ranatra*. It extends dorsally, like the pleural apophyses of the aquatic forms. Among the semi-aquatic bugs, according to Larsén (1945a and b), the mesothoracic pleural apophysis is absent in *Velia*, small in *Gerris*, and well developed in *Hydrometra*; among the Geocorisae it is variable in both size and position (Larsén, 1945b). Malouf's (1933) figure of the mesothoracic pleural apophysis in the terrestrial bug *Nezara* shows it to be fairly small and medially directed.

In a few other features of the thoracic skeleton, *Gelastocoris* resembles the Hydrocorisae, Amphibicorisae, or Geocorisae.

Larsén (1945b) found a distinct separation between the metathoracic scutum and scutellum only in the aquatic and semi-aquatic bugs. Although Akbar (1957) described a clear separation between these two regions in the metanotum of *Leptocoris*, a terrestrial bug, it seems that his interpretation is open to criticism; the part termed the "scutum" by him seems to be the notum, while his "scutellum" (as shown in his Fig. 66) resembles the postnotum. Malouf (1933) also incorrectly described a distinct metascutum and metascutellum in *Nezara*, as Larsén (1945b) has pointed out. On the gelastocorid metanotum there is a fairly definite groove which may represent a scutoseutellar suture; if this interpretation is correct, this character links the gelastocorids with both the Hydrocorisae and the Amphibicorisae.

Larsén (1945b) also reported the prothoracic postcoxal bridge to be broader than the precoxal bridge in the majority of Hydrocorisae; this is also the case in *Gelastocoris*. In the Geocorisae and Amphibicorisae, either the precoxal bridge is the broader of the two or both bridges are equal in size. This does not serve to distinguish the Hydrocorisae as a whole, however, since in *Notonecta* and *Corixa*, according to Larsén, the postcoxal bridge is narrower than the precoxal.

Larsén (1945b) found that although the metathoracic subalare is present in most terrestrial bugs it is absent in most aquatic (with the exception of *Notonecta*) and semi-aquatic forms. The presence of a metathoracic subalare in *Gelastocoris* is, therefore, a character most commonly found in the Geocorisae; this sclerite is, however, much reduced in *Gelastocoris*.

The thoracic musculature does not shed as much light on the phylogenetic problem as does the thoracic skeleton. Larsén's comparative study revealed very few differences between the three major heteropteran groups on the basis of musculature. Three generalizations can be made, however. First, the two dorsal longitudinal muscles of the heteropteran metathorax ("Mm. metanoti primus" and "secundus" of Larsén, 1945a) are absent in all the Hydrocorisae examined by that author, while at least one of the two is present in *Salda*, in all the Amphibicorisae, and in all but two of the Geocorisae. *Gelastocoris* resembles the aquatic bugs in this respect, since it lacks both metathoracic dorsal longitudinal muscles. Secondly, the ventral longitudinal

muscle of the abdomen (*M. ventralis abdominalis* of the present study) is well developed in all Larsén's Hydrocorisae and in *Salda*, but is weak or absent in most of the semi-aquatic and terrestrial forms examined by him. Here again, *Gelastocoris* resembles the Hydrocorisae. Thirdly, a *M. coxa-subalaris* is present in both the mesothorax and the metathorax of most of the terrestrial bugs studied by Larsén, but is absent in the aquatic and semi-aquatic forms, the only exception being its presence in the metathorax of *Notonecta*. The presence of this muscle in the metathorax of *Gelastocoris* links this bug with the Geocorisae; the link is not very strong, however, since *Notonecta* also possesses this muscle in the metathorax, and since the muscle is absent in the mesothorax of *Gelastocoris*.

In general, therefore, the skeleton and musculature of the thorax of *Gelastocoris* bear more resemblance to those of the Hydrocorisae than to those of the Amphibicorisae or Geocorisae. This is in agreement with the conclusions reached in a previous study of the gelastocorid head (Parsons, 1959), and supports the phylogenetic theory of China (1955). Similarities to the aquatic bugs are seen in the structure of the metatergal sclerites, the presence of distinct pleural ridges in all three segments, the size of the mesothoracic and metathoracic epimera, the degree of development of the mesothoracic pleural apophyses, and the breadth of the prothoracic postcoxal bridge. Further resemblances to the aquatic Heteroptera are the absence of metathoracic dorsal longitudinal muscles and the presence of *M. ventralis abdominalis*. The gelastocorids also resemble both the Hydrocorisae and the Amphibicorisae in the separation between the metascutum and the metascutellum. Only two features of the gelastocorid thorax are atypical of the Hydrocorisae; in their possession of a metathoracic subalare and subalar muscle, they resemble the Geocorisae (although these two characters are also found in *Notonecta*, which is definitely one of the Hydrocorisae). It must be borne in mind, however, that there are exceptions in the literature to all of the above generalizations, and that these are not clear-cut distinctions.

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EXPLANATION OF FIGURES

In the figures, the membranes, the muscles, the tendons, and the cut edges of the skeleton are unstippled, while the skeletal surfaces are either stippled or blackened. The muscles are indicated by the numbers given in pages 329-346. Each major tendon is indicated by a "T" followed by the number of the muscle attaching to it; when more than one muscle attaches to a tendon, the tendon's number is that of the lowest-numbered muscle. The numeral II after an abbreviation indicates a mesothoracic structure, while the numeral III indicates a metathoracic structure.

The abbreviations used in the figures are as follows:

- 1, 2, or 3 A — first, second or third anal vein
- AB — anterior basicoxite
- AC — axillary cord
- AF — anteromedial flap of stink groove
- AM — abdomen
- AP — anterolateral abdominal process
- AW — anterior notal wing process
- 1, 2 3, or 4 AX — first, second, third or fourth axillary sclerite
- BR — basicostal ridge
- BS — basicostal suture
- C+CS — costa plus subcosta
- CC — coxal cavity
- CL — coxal cleft
- CM — cervical membrane
- CO — corium
- CP — coxal process
- CU — cubitus
- CV — clavus
- CW — claw
- CX — coxa
- EL — posterior epimeral lobe
- EM — embolium
- EP — epimeron
- EPS — supracoxal lobe of epimeron
- ES — episternum
- ESS — supracoxal lobe of episternum
- EV — evaporating surface
- F — furea
- FA — fureal apodeme
- FE — femur